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Differential motion processing between species facing Ternus–Pikler display: Non-retinotopic humans versus retinotopic pigeons

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ABSTRACT

Retinotopic encoding is preserved in primate visual cortex. However, several physiological and psychophysical studies have revealed that visual processes can be disengaged from retinotopic coordinates. We examined whether this non-retinotopic processing is common to humans and pigeons, two visually dominant vertebrate species with similar retinotopic organizations in their brains. We used a variant of Ternus–Pikler stimulus as a litmus test for non-retinotopic processing. Six humans and four pigeons were required to discriminate the rotational direction of a target disk placed among linearly arranged non-rotating disks. When all disks flickered in synchrony (a blank screen was inserted between the stimulus presentations) and moved in tandem back and forth, target localization was hampered in humans but not pigeons (Experiment 1). The duration of the blank screen (Experiment 2) and the connection between the disks (Experiment 3) did not affect the pigeons' performance. These results suggest that non-retinotopic processing in human vision is not a feature of pigeon vision, which is instead strictly retinotopic in case of motion. This may reflect the different mechanisms for stimulus selection in both species, in which local motion signals were pooled at later stages of visual processing in humans, but the signals were selected at early stages in pigeons.

1. Introduction

When humans see the world, the environment is projected onto the retina. The spatial relationship among environmental elements corresponds to that of photoreceptors in the retina. This point-to-point retinotopic encoding is preserved in the primate striate cortex, in which neurons have small receptive fields (Adams & Horton, 2003; Dow, Vautin, & Bauer, 1985; Engel, Glover, & Wandell, 1997; Tootell et al., 1982). In contrast, simple retinotopic encoding is not preserved in extra-striate cortex, where neurons have relatively large receptive fields and complex response properties (Tootell et al., 1998). Several physiological and psychophysical studies have revealed that visual processes can be disengaged from the retinotopic coordinates. For example, Duhamel et al. (1997) found that a monkey's parietal neurons respond to a position in space irrespective of gaze direction. This spatial invariance of the neurons appears to be one of the underlying mechanisms for keeping our perceptual world stable irrespective of eye movements. As a psychophysical illustration, Harrison et al. (2013) showed that an object's features are processed at a remapped location after eye movement. This predicted re-mapping also enables our perceptual world stable. These results suggest the existence of non-retinotopic as well as retinotopic processing. However, it is unknown whether the non-retinotopic processing of the primate visual system is shared with other animal species.

Here we investigated whether birds, the most visually-dominant vertebrate groups in the animal kingdom, share non-retinotopic processing with primates. We studied pigeons because of the abundant behavioral and physiological data concerning their visual processes. Like the primary visual cortex in primate brain, retinotopic encoding is preserved in the optic tectum (TeO), which is the visual center in pigeon brain (Hamdi & Whitteridge, 1954; Mcgill, Powell, & Cowan, 1966). However, neurons in nucleus rotundus (nRt), which receives visual information from TeO, are not organized retinotopically (Marín et al., 2003). From this anatomical perspective, visual inputs could be processed retinotopically at early stages of visual information stream and later processed non-retinotopically in the avian brain, as in the primate brain.

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Few behavioral studies have segregated non-retinotopic from retiotopic processing in pigeons. Comparative research has revealed that pigeons share various visual processes with humans including object recognition (Kirkpatrick-Steger & Wasserman, 1996) and perception of various visual illusions (Fujita, Blough, & Blough, 1991; Nakamura et al., 2006). Although these studies might lead to the prediction that non-retinotopic visual processing is also shared between humans and pigeons, some demonstrations of functional differences between the two species contradict this view. Functional differences have been found especially in motion processing. Ushitani, Fujita, and Sato (2004) showed that pigeons do not organize motions of two objects, in contrast to humans. The authors trained pigeons to discriminate the direction of a moving dot (a target). Discrimination performance was not affected by an adjacent dot moving in a direction 45 deg different from the target dot. In this situation, humans typically organize the motions to perceive the target moving relative to the adjacent dot, and consequently discrimination performance is hampered. Bischof et al. (1999) found that motion sensitivity of pigeons is inferior to that of humans. The authors trained both species to discriminate coherent motion from random motion in dynamic random dot displays. Resulting coherence thresholds were higher for pigeons than for humans. These studies suggest that pigeons are highly dependent on the retinotopic coordinates; in the first study retinotopic motion processing of the target was unaffected by the motion of the adjacent dot, while in the second study the retinotopic local motion signals were not integrated into a global percept. Thus, anatomical and behavioral perspectives diverge, leaving open the question whether non-retinotopic processing exists in pigeon vision.

In the present study, we examined whether pigeons depend on non-retinotopic or retinotopic processing in perceiving motion using a previously tested procedure. We employed a variant of the Ternus–Pikler stimulus used by Boi et al. (2009), who introduced a simple technique to distinguish non-retinotopic from retinotopic processing and demonstrated that a motion process could occur non-retinotopically in humans. Three horizontally aligned white disks were presented for 200 ms. After an ISI (inter-stimulus interval) of variable duration the rightmost disk was shifted towards the leftmost, or vice versa, and after another ISI the sequence started over again (Fig. 1). In one of the three disks (a target disk), a red dot was presented in each frame, moving along a clockwise or counterclockwise rotational trajectory. The dot made a complete rotation every four frames (90 deg per frame). The position of the rotating disk was fixed throughout the sequence. The other two disks contained a red dot in the center.

Human perception markedly changes depending on the ISI. With short ISIs, humans typically perceive the outmost disk as jumping back and forth, and they easily discriminate the rotation direction of the target (Fig. 1a, see Movie 1). With relatively long ISIs (longer than 100 ms), however, humans perceive the three disks as moving back and forth horizontally in a group (Fig. 1b, see Movie 2). The perception of the group motion impairs attention to the target and makes the rotation discrimination difficult even though the spatial configurations of the three disks are identical as when presented with short ISIs. This effect shows up independent of eye movements; there was little pursuit or predictive eye movements (Boi et al., 2009). When the outmost disk is deleted so that only two disks are presented, there is no dissociation in discriminability of the target rotation between long and short ISIs because no group motion is perceived (Fig. 1c, see Movie 3). As the absolute position of the target is invariant throughout the sequence, target rotation is processed retinotopically. Under a specific spatio-temporal interaction (three disks × long ISI), however, this retinotopic processing is disrupted by the perceived group motion, which we define as non-retinotopic processing. We compared humans and pigeons using the interaction between the ISI and number of the disks on task performances as an indicator of non-retinotopic processing.

2. Experiment 1

2.1. Material and methods

2.1.1. Subjects

2.1.1.1. Humans. Six adult humans (*Homo sapiens*) including one of the authors (S.O.) from Kyoto University voluntarily participated. They ranged in age from 21 to 31 years, and had normal or corrected-to-normal vision. All subjects participated in all experiments. All experiments were conducted in accordance with the ethical guidelines in the Declaration of Helsinki and informed consent was obtained prior to participation.

2.1.1.2. Pigeons. Four homing pigeons (*Columba livia*) were used. They were maintained at or over 85% of their free-feeding weights throughout the study period. They were housed in individual cages in a 12:12 h light/dark cycle and with free access to grit and water. All four pigeons participated in all experiments.

2.1.2. Apparatus

2.1.2.1. Humans. Stimuli were presented on a 24-in. touch sensitive LCD monitor (Iiyama, T2250MTS) running at a refresh rate of 60 Hz and with a resolution of 1920 × 1080 pixels. A personal computer (Dell, Optiplex 980) controlled the experiments and collected the data. Experimental programs were written in Microsoft Visual Basic 6.0.

2.1.2.2. Pigeons. The experiments were conducted in four identical operant chambers (35 cm × 35 cm × 35 cm) installed with LCD monitors (EIZO, FlexScan L367) and touch sensitive frames (Touch

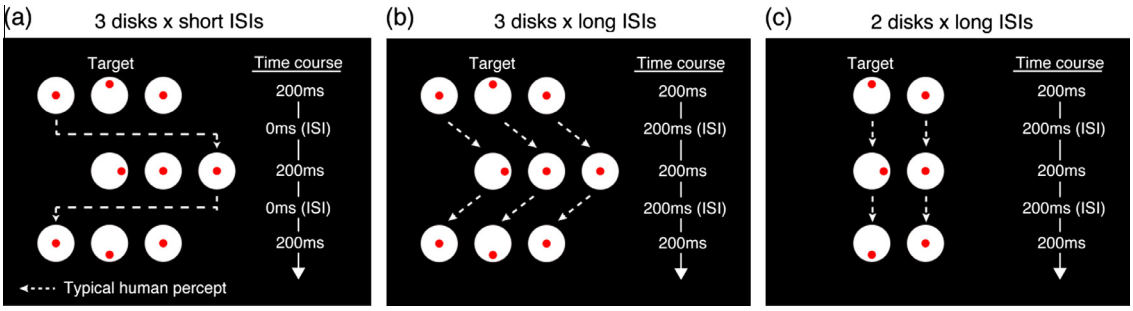

Fig. 1. Ternus–Pikler stimuli in the present study. (a) With three disks and no ISI, human subjects typically perceive only the outer disk moving back and forth, and easily discriminate the rotational direction of the target disk (see Movie 1). (b) With three disks and long ISIs, three disks are perceived moving as a group in a horizontal, back-and-forth pattern. Discrimination of the rotational direction of the target disk is hampered (see Movie 2). (c) With two disks, no group motion is perceived and the discrimination is easy even with the long ISIs (see Movie 3).

Panel Systems, UniTouch). All stimuli were presented on the monitor. The refresh rate of each monitor was 60 Hz and resolution was 1024 × 768 pixels. A grain hopper delivered food reward through an opening on the left-side wall of each chamber. Built-to-order personal computers (Mouse Computer, LM-i500SC) controlled the experiments and collected the data. The same programs as in the human experiments were used.

2.1.3. Stimuli

In each trial, the two stimuli described above were presented on both sides of the diagonal line of the display to prevent perception of the stimuli as a unitary stimulus (Fig. 2). One stimulus consisted of a disk rotating clockwise (target) and non-rotating disks (inducer), and the other consisted of a disk rotating counter-clockwise (distractor) and the inducers. Each disk was 1.6 cm in diameter and the distance between the disks was 0.8 cm for humans. The corresponding measures for pigeons were 1.0 cm and 0.5 cm. Although human and pigeon subjects could view the display freely, the viewing distance was approximately 40 cm and 9 cm, respectively. The distance for pigeons was comparable to that in Bischof et al. (1999). Each disk corresponded to 2.3 deg and 6.4 deg of visual angle for humans and pigeons, respectively. The size of the disks was determined so that the entire array was within the 37 deg of the frontal visual field of the pigeons (Mcfadden & Reymond, 1985).

2.1.4. Procedure

2.1.4.1. Humans. Human subjects performed a two-alternative forced-choice task. Each subject was required to touch the target disk rotating clockwise using the right index finger. A touch to either the target disk or the distractor disk was effective. Touches to non-rotating disks were ineffective. The subjects were instructed to respond as quickly and accurately as possible. They were then given 32 warm-up trials to learn the task using the same stimuli as in the experiments.

Each trial started with a white warning signal (1.0 cm × 1.0 cm) appearing at the center of the display. Touching this signal immediately replaced it with the stimulus display described above. Responses to the target disk were followed by a chime sound, whereas those to the distractor disk were followed by a buzzer sound. The inter-trial interval was 500 ms (Fig. 2). The ISI was either 200 ms or 0 ms. Each stimulus contained either two or three disks; the outmost disk was excluded in the former case. Each inducer disk had a red dot in the center in one half of the trials (inducer dot present trials), and no dot in the other half (inducer dot absent trials). The inducer dot absent trials were used as a baseline for rotation discrimination. The two stimuli were presented at upper left and lower right or upper right and lower left in each trial. The target appeared on either the left or right stimulus at random, and the distractor appeared on the opposite side. Therefore, one out of 32 different stimulus configurations (2 ISIs × 2 numbers of disks × 2 inducer types × 2 stimulus arrangements × 2 target positions) was randomly presented on every trial. Each session consisted of 4 blocks of 32 trials. Each human subject was tested in only one session.

2.1.4.2. Pigeons. Pigeons eventually performed the same task as human subjects, but with some minor modifications. Responses to the target disk were followed by 2.5 s of food access, whereas responses to the distractor disk were followed by 10 s timeout. Inter-trial intervals were 5 s (Fig. 2). Pigeons were trained in several stages before exposure to the final task. First, they were trained to peck at the target disk presented with the distractor disk, with no inducer disks present. The dots on the disks made complete rotations every eight frames (45 deg per frame). The ISI was always 0 ms. After the pigeons scored higher than 80% correct for two sessions, the step between the frames was changed to 90 deg. This criterion was maintained in all subsequent pre-training stages. Once criterion was reached, the ISI was lengthened to 200 ms for half of the trials. In the final stage of pre-training, blank inducers accompanied the target and the distractor. At this stage the task and stimulus setting was identical to that in inducer dot absent trials of the test. Pigeons were tested on the same experimental task as humans after reaching criterion. Each session consisted of 4 blocks of 32 trials, as with human. The pigeons received 10 sessions.

2.2. Results and discussion

2.2.1. Humans

Fig. 3 shows the mean error rates (bar graphs) and the response times averaged for correct choices (line graphs) in each condition for humans. The overall error rate was 2.3%, and little difference was found among conditions. A three-way repeated-measures

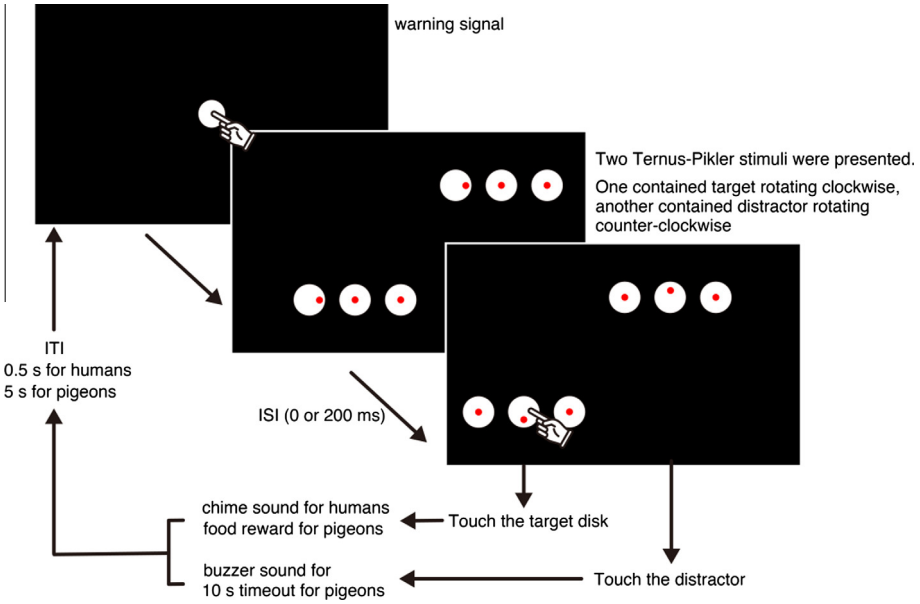

Fig. 2. Trial sequence for the experiments.

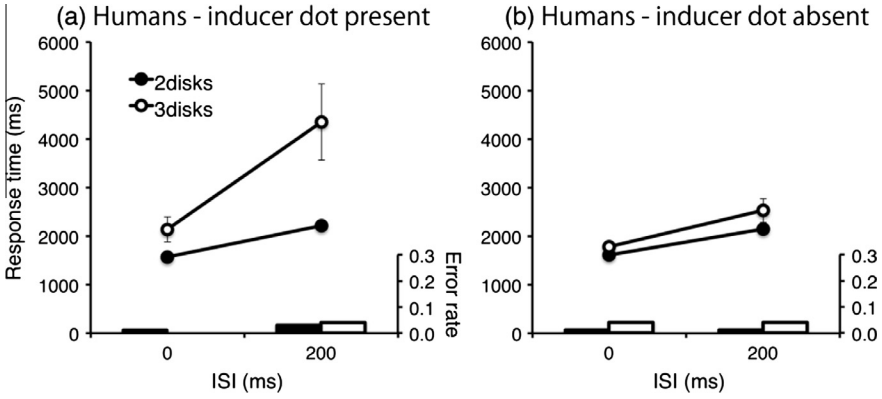

Fig. 3. Mean error rates and mean response times in (a) inducer dot present trials and in (b) inducer dot absent trials in Experiment 1 for human subjects. Bars at the bottom of the figures show the error rates. Closed circles and bars represent trials with two disks, and open circles and bars represent trials with three disks. Error bars indicate *SEM*.

analysis of variance (ANOVA) with the ISI, the number of disks, and inducer type revealed no significant main effects [ISI: $F(1,5) = 2.50$, $p = .175$, $\eta p^2 = 0.33$; the number of disks: $F(1,5) = 3.76$, $p = .110$, $\eta p^2 = 0.43$; inducer type: $F(1,5) = 0.36$, $p = 0.572$, $\eta p^2 = 0.07$].

Unlike the error rate, response times varied markedly across conditions. In inducer dot present trials (left panel), response times with three disks were more affected by the ISI than those with two disks. In contrast, response times with three and two disks were almost the same in inducer dot absent trials. A three-way ANOVA revealed significant main effects of ISI [$F(1,5) = 26.92$, $p = .004$, $\eta p^2 = 0.84$], the number of disks [$F(1,5) = 8.39$, $p = .034$, $\eta p^2 = 0.63$], and inducer type [$F(1,5) = 9.15$, $p = .029$, $\eta p^2 = 0.65$]. The interaction among the three factors was also significant [$F(1,5) = 7.34$, $p = .042$, $\eta p^2 = 0.59$]. The same ANOVA revealed a simple interaction between ISI and the number of disks in inducer dot present trials [$F(1,5) = 10.33$, $p = .024$, $\eta p^2 = 0.67$], but no interaction in inducer dot absent trials [$F(1,5) = 1.47$, $p = .279$, $\eta p^2 = 0.28$]. A post hoc analysis using Scheffe's procedure for inducer dot present trials revealed a simple main effect of the ISI with three disks [$F(1,5) = 72.07$, $p < .001$, $\eta p^2 = 0.94$], and with two disks [$F(1,5) = 16.54$, $p = .010$, $\eta p^2 = 0.77$].

The strong interaction between ISI and the number of disks suggests non-retinotopic processing in inducer dot present trials. Humans perceived the three disks as moving back and forth horizontally in a group and this perceived group motion disturbed the rotation discrimination. As a consequence, the response time for the combination of 200 ms ISI and three disks was much longer than for other combinations. The small increase in response time even with two disks was simply because it took longer to complete rotation with 200 ms ISI than with 0 ms ISI. The absence of an interaction in inducer dot absent trials indicates that non-retinotopic processing did not operate with the distinctive target. In that case human subjects kept their attention to the target location. These results show that non-retinotopic processing interferes with retinotopic rotation processing under the specific interaction between the spatial (three aligned disks) and temporal configuration (long ISI). These results also confirm that the Ternus–Pikler stimulus is appropriate for testing non-retinotopic processing in human vision, as shown in Boi et al. (2009).

2.2.2. Pigeons

Fig. 4 shows the mean error rates (bar graphs) and response times averaged for correct choices (line graphs) in each condition for pigeons. The overall error rate was 19.2%. The error rate for the long ISI was higher than for the short ISI, but the error rate was independent of the number of the disks. Because the general trends in the data of all four pigeons appear similar, we compiled the group data by sessions for each condition and used the group data for statistical analysis. A three-way repeated-measures ANOVA with ISI, the number of disks, and inducer type revealed significant main effects of ISI [$F(1,9) = 182.03$, $p < .001$, $\eta p^2 = 0.95$] and inducer type [$F(1,9) = 10.77$, $p = .010$, $\eta p^2 = 0.54$], but not of the number of disks [$F(1,9) = 0.30$, $p = .599$, $\eta p^2 = 0.03$], and no three-way interaction [$F(1,9) = 0.02$, $p = .910$, $\eta p^2 = 0.01$]. No interactions were significant, including that between ISI and the number of disks [$F(1,9) = 2.97$, $p = .119$, $\eta p^2 = 0.25$].

For comparing pigeons with humans, we used response times as a primary measure. Response time correlated positively with error rate, as can be seen in Fig. 4. Response time was longer for the long ISI than for the short ISI, and was also longer in inducer dot present trials than in inducer dot absent trials. The increase in response time was similar in the two- and three-disk conditions. A three-way repeated measures ANOVA revealed significant main effects of ISI [$F(1,9) = 403.94$, $p < .001$, $\eta p^2 = 0.98$] and inducer type [$F(1,9) = 105.84$, $p < .001$, $\eta p^2 = 0.92$], but not of the number of disks [$F(1,9) = 3.48$, $p = .095$, $\eta p^2 = 0.28$], and no three-way interaction [$F(1,9) = 2.25$, $p = .167$, $\eta p^2 = 0.20$]. No interaction was significant, including that between ISI and the number of disks [$F(1,9) = 0.28$, $p = .607$, $\eta p^2 = 0.03$].

The lack of interaction between ISI and the number of disks strongly suggests that the target rotation was exclusively processed retinotopically by the pigeons. Because the frontal visual field of pigeons is small (Mcfadden & Reymond, 1985), our subjects might have viewed only the target and disregarded the flanked inducers. This is unlikely, however; the significant difference between inducer types indicated that inducers similar to the target in appearance disturbed the rotation discrimination of the target. It is likely that although the pigeons viewed all of the disks like humans, their motion processing was strictly retinotopic, unlike in humans.

2.2.3. Effect of training

Whereas our human subjects experienced limited trials, the pigeons experienced extended training and test trials. This differential exposure to the experiments might account for the divergent results between humans and pigeons. To test this possibility, we gave two human subjects out the six who participated in Experiment 1 an additional nine sessions. We divided all ten sessions into two five-session blocks. The interaction between the ISI and the number of disks still remained in the second block. A three-way ANOVA with ISI, the number of disks, and session block (first or second) as factors revealed significant main effects of ISI [$F(1,4) = 211.40$, $p < .001$, $\eta p^2 = 0.98$], the number of disks [$F(1,4) = 182.52$, $p < .001$, $\eta p^2 = 0.98$], and block [$F(1,4) = 7.93$,

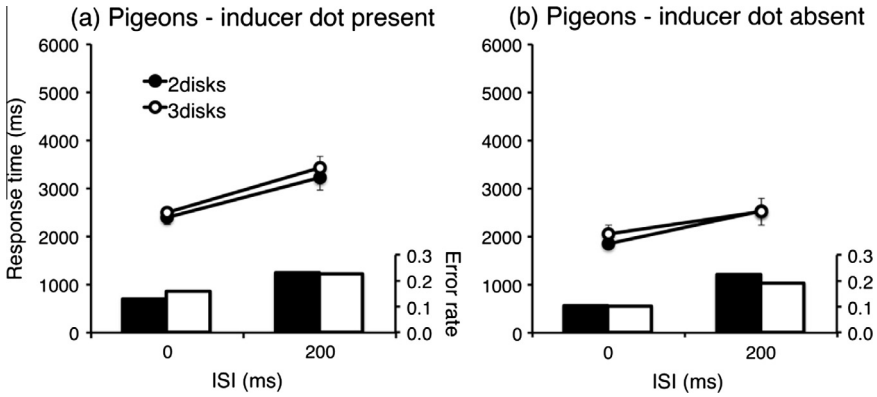

Fig. 4. Mean error rates and mean response times in (a) inducer dot present trials and in (b) inducer dot absent trials in Experiment 1 for pigeon subjects.

$p = .048$, $\eta p^2 = 0.66$]. The interaction between ISI and the number of disks was significant [$F(1,4) = 71.44$, $p = .001$, $\eta p^2 = 0.95$], but the three-way interaction was not [$F(1,4) = 2.95$, $p = .161$, $\eta p^2 = 0.42$]. Thus, the interaction between ISI and number of disks was unaffected by repeated exposure to the stimuli. Human performance was affected by non-retinotopic processing even after extended sessions.

We conducted the same analysis on pigeon data. A three-way ANOVA revealed a significant main effect of ISI [$F(1,4) = 231.92$, $p < .001$, $\eta p^2 = 0.98$], but no significant effect of the other two factors [the number of disks: $F(1,4) = 0.30$, $p = .264$, $\eta p^2 = 0.26$; session block: $F(1,4) = 0.54$, $p = .502$, $\eta p^2 = 0.12$]. There was no interaction between ISI and number of disks in either the first or the second session block. The motion processing in the pigeons was retinotopic, irrespective of training.

3. Experiment 2 – effect of intermediate ISIs

The results of Experiment 1 suggest that the motion discrimination in pigeon vision may depend on retinotopic processing, whereas that in human vision involves non-retinotopic processing at a particular spatio-temporal interaction. Experiment 2 examined the effects of a variety of ISIs on task performance. The temporal properties of pigeons' visual perception are different from those of humans due to structural differences in the visual systems of the two species. For example, critical flicker frequency in pigeons is much higher than in humans (approximately 140 Hz, Hendricks, 1966), and the onset of a second target affects first target localization by pigeons following a peculiar time course (Cook, Katz, & Blaisdell, 2012). These results suggest that non-retinotopic processing by pigeons may have a different temporal property from that by humans. In Experiment 1, we used only 0 ms and 200 ms as the ISI values. We tested ISIs of 0, 50, 100, 150, and 200 ms in Experiment 2.

3.1. Procedure

The experimental task was the same as in Experiment 1 except that the ISI was 0, 50, 100, 150, or 200 ms, and inducer dot absent trials were omitted. Thus, each human subject received 1 session of 160 trials: 5 ISIs × 2 numbers of disks × 2 stimulus arrangements × 2 target positions × 4 blocks. The pigeons received 10 sessions with the same stimulus configurations as humans.

3.2. Results and discussion

Fig. 5 shows the mean error rate and average correct response times for humans and pigeons. The mean error rate was 2.3% for humans and 11.3% for pigeons. We used response time as the primary measure for comparing the performance between the two species because there was no statistical difference between conditions in humans' error rate data. Although there was a strong interaction between ISI and the number of disks for humans, there was no interaction for pigeons, as in Experiment 1.

We applied three-way ANOVAs for each species. For humans, significant main effects of ISI [$F(4,20) = 10.26$, $p = .010$, $\eta p^2 = 0.67$] and the number of disks were revealed [$F(1,5) = 7.69$, $p = .039$, $\eta p^2 = 0.60$], along with a significant interaction between the two factors [$F(4,20) = 4.73$, $p = .008$, $\eta p^2 = 0.49$]. Post hoc analyses revealed simple main effects of ISI with three disks [$F(4,20) = 18.94$, $p < .001$, $\eta p^2 = 0.79$], as well as with two disks [$F(4,20) = 7.49$, $p = .019$, $\eta p^2 = 0.60$]. The steep inclination of the response time with three disks was similar to the result in Experiment 1. For pigeons, a significant main effect of ISI was found [$F(4,36) = 25.15$, $p < .001$, $\eta p^2 = 0.74$]; however, there was no significant main effect of the number of disks [$F(1,9) = 3.49$, $p = .095$, $\eta p^2 = 0.28$] and no significant interaction [$F(4,36) = 0.58$, $p = .676$, $\eta p^2 = 0.06$].

The interaction between the two factors and a linear increase in the difference between the two- and three-disks conditions suggest that non-retinotopic processing in human vision may begin to operate depending on the duration of ISI, like other psychological functions. In contrast, there was no interaction in pigeons, recalling the results in Experiment 1. The consistent lack of an interaction indicates that motion processing in pigeon vision may be strictly retinotopic, and that non-retinotopic processing does not interfere with retinotopic processing irrespective of temporal properties.

4. Experiment 3 – effect of spatial grouping

In Experiment 3, we examined the effect of spatial grouping on non-retinotopic processing using a stimulus in which three disks were connected to each other by a white horizontal bar. Experiments 1 and 2 showed a strong interaction between ISI and the number of disks in humans. This may arise because human visual attention shifted towards the center among the three disks with the long ISI. Human subjects may have perceived the three disks as a unit. If perceived unity of the objects is an important factor for non-retinotopic processing, explicit connection of the three disks should enhance the interaction.

In contrast to humans, there was no interaction in pigeons. We argued that the lack of the interaction is due to pigeons' strong dependence on the retinotopic coordinates of the target. However, another explanation is possible. Many previous reports failed to show amodal completion in pigeons. For instance, Ushitani,

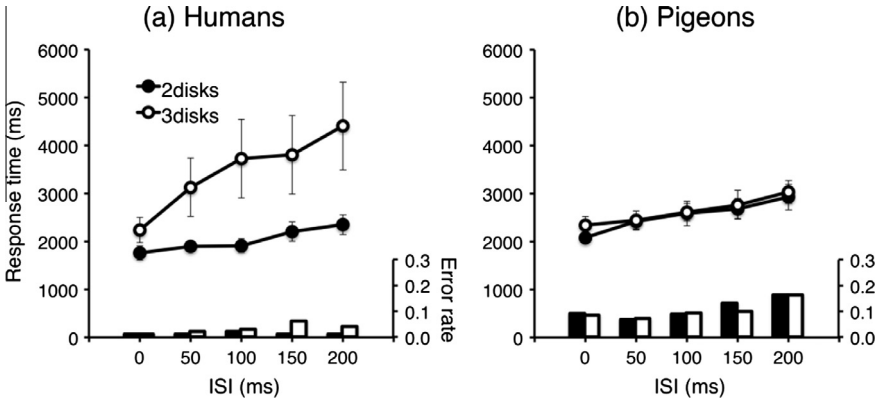

Fig. 5. Mean error rates and mean response times in Experiment 2 (a) for humans and (b) for pigeons.

Fujita, and Yamanaka (2001) reported that pigeons do not complete the occluded portion of a moving bar (but see Nagasaka, Hori, & Osada, 2005). In that study, pigeons regarded two portions of an object separated by a rectangle as different objects. This lack of spatial grouping could also explain the results in Experiments 1 and 2. The flanked inducers would not disturb the rotation discrimination if the pigeons perceived the three disks as independent. To examine this possibility, we compared the performance between two conditions: three disks connected to each other in one condition and separated in another. If the interaction appears in the former case, it becomes clear that the lack of the interaction in the first two experiments can be explained by the lack of the spatial grouping and that non-retinotopic processing could operate in pigeon vision.

4.1. Procedure

The experimental task was the same as in Experiment 1. The inducer dot absent trials were omitted, as in Experiment 2. In half of the trials three or two disks were connected to each other by a single white bar. In the other half, the stimuli were exactly the same as in Experiments 1 and 2. Each human subject received 1 session consisting of 192 trials: 2 ISIs × 2 numbers of disks × 2 connection types (connected or non-connected) × 2 stimulus arrangements × 2 target positions × 6 blocks. The pigeons received 10 sessions of the same configurations as humans.

4.2. Results and discussion

4.2.1. Humans

Fig. 6 shows the mean error rate and average correct response times for humans. The overall error rate was 7.1%. In contrast to the results of Experiments 1 and 2, the error rate varied with condition. There was little difference among conditions in the non-connected condition (left panel), similar to Experiment 1. However, the error rate for the combination of 200 ms ISI and three disks was higher than for other combinations in the connected condition (right panel). A three-way ANOVA revealed main effects of connection type [$F(1,5) = 25.73$, $p = .004$, $\eta p^2 = 0.84$], ISI [$F(1,5) = 61.25$, $p < .001$, $\eta p^2 = 0.92$], and the number of disks [$F(1,5) = 122.55$, $p < .001$, $\eta p^2 = 0.96$]. The three-way interaction was also significant [$F(1,5) = 26.06$, $p = .004$, $\eta p^2 = 0.84$]. Further analyses revealed a significant interaction between ISI and the number of disks in the connected condition [$F(1,5) = 67.99$, $p < .001$, $\eta p^2 = 0.93$] and the non-connected condition [$F(1,5) = 7.83$, $p = .038$, $\eta p^2 = 0.61$]. Post-hoc analyses using Shaffer's procedure revealed a simple main effect of ISI only for three disks in the connected condition [$F(1,5) = 71.25$, $p < .001$, $\eta p^2 = 0.93$] and the non-connected condition [$F(1,5) = 7.06$, $p = .045$, $\eta p^2 = 0.59$]. The large effect size in the connected condition indicates that connection makes the three disks into a unit and causes the human subjects to shift their attention to the center of the unit. The results also suggest that non-retinotopic processing in human vision depends on the unity of the objects in addition to the spatio-temporal properties of the object.

A similar tendency was observed in the response times. A three-way ANOVA revealed significant main effects of ISI [$F(1,5) = 13.12$, $p = .015$, $\eta p^2 = 0.72$], the number of disks [$F(1,5) = 9.21$, $p = .029$, $\eta p^2 = 0.65$], and an interaction between the two factors [$F(1,5) = 7.30$, $p = .042$, $\eta p^2 = 0.59$]. This interaction again indicates non-retinotopic processing. A marginal main effect of connection type was found [$F(1,5) = 4.78$, $p = .090$, $\eta p^2 = 0.49$]. This weak effect may reflect a speed-accuracy trade off. The error rates were near to zero irrespective of the conditions in Experiments 1 and 2. The human subjects responded accurately, and consequently the difference between conditions was seen in the response time. By contrast, the error rate in Experiment 3 was 7.1%, and consequently the difference appeared in the error rate rather than response time.

4.2.2. Pigeons

Fig. 7 shows the mean error rate and average correct response times for pigeons. The overall error rate was 17.9%. There was no significant interaction between ISI and the number of disks for either connection type. A three-way repeated measures ANOVA revealed significant main effects of connection type [$F(1,9) = 111.22$, $p < .001$, $\eta p^2 = 0.93$] and ISI [$F(1,9) = 29.61$, $p < .001$, $\eta p^2 = 0.77$], and a marginal main effect of the number of disks [$F(1,9) = 4.80$, $p = .056$, $\eta p^2 = 0.35$]. The interaction among the three factors was not significant [$F(1,9) = 0.73$, $p = .414$, $\eta p^2 = 0.08$], nor was the interaction between ISI and the number of disks [$F(1,9) = 0.15$, $p = .710$, $\eta p^2 = 0.02$]. Although the error rate in the connected condition was higher than in the non-connected condition, connection type failed to affect the interaction between ISI and the number of disks.

Response times varied similarly to error rates. A three-way repeated measures ANOVA revealed main effects of the connection type [$F(1,9) = 17.65$, $p = .002$, $\eta p^2 = 0.66$], ISI [$F(1,9) = 146.28$, $p < .001$, $\eta p^2 = 0.94$], and the number of disks [$F(1,9) = 10.32$, $p = .011$, $\eta p^2 = 0.53$], but no interaction among the three factors [$F(1,9) = 0.72$, $p = .418$, $\eta p^2 = 0.07$]. The interaction between ISI and the number of disks was not significant [$F(1,9) = 0.12$, $p = .741$, $\eta p^2 = 0.01$].

Both the error rate and the response time showed no interaction between ISI and the number of disks in pigeons. The results indicate that non-retinotopic processing failed to interfere with retinotopic motion processing in pigeon vision even though the three disks were physically connected. We conclude that the lack of

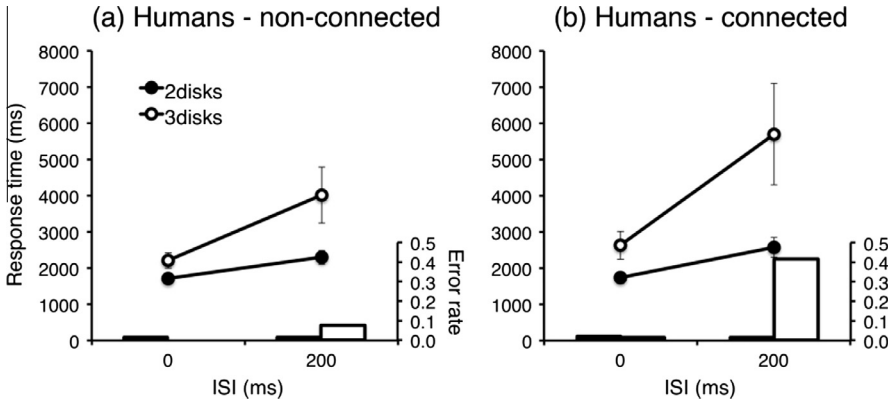

Fig. 6. Mean error rates and mean response times for (a) non-connected condition and for (b) connected condition in Experiment 3 for human subjects.

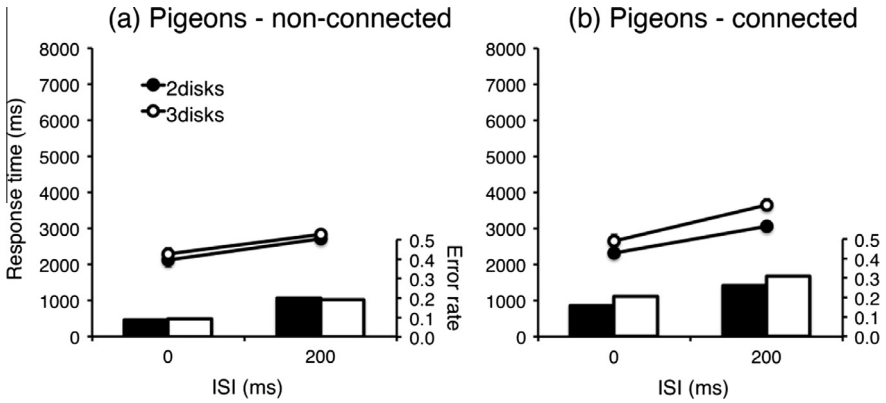

Fig. 7. Mean error rates and mean response times for (a) non-connected condition and for (b) connected condition in Experiment 3 for pigeon subjects.

the non-retinotopic processing in pigeons is real and not due to a lack of spatial grouping.

5. General discussion

5.1. Non-retinotopic processing in human vision

We examined whether humans and pigeons share non-retinotopic processing using variants of the Ternus–Pikler stimulus described in Boi et al. (2009). Target localization deteriorated with the combination of long ISI and three disks in human subjects. In this condition, humans appear to perceive the three disks as moving in tandem back and forth. Although the physical position of the target disks was invariant, the perceived group motion prevented the subjects from keeping their attention to the target location. We conclude that retinotopic motion processing (target rotation) was disturbed by non-retinotopic motion processing (perceived group motion). Moreover, we made several new discoveries about non-retinotopic processing in Experiments 2 and 3. First, non-retinotopic processing in human vision may begin to operate depending on the duration of ISI. Second, the perception of unity of the objects facilitates non-retinotopic processing.

Boi et al. (2009) proposed a two-stage model in which the synchronized motion with grouped disks is established in the first stage and then a non-retinotopic framework is provided in the second. In contrast, Pooresmaeili et al. (2012) proposed a simple motion computation model, in which motion is analyzed by optimally tuned filters oriented in space and time. This model extracts the directional motion energy by directional filtering of the 3D Fourier spectrum of the Ternus–Pikler stimulus, in which three horizontally aligned grating windows were perceived as moving in tandem. The model predicts the psychophysical performance of humans with an optimal size of the directional filter. The effect of the perceived unity of the objects involved in the non-retinotopic interference we found in Experiment 3 challenges Pooresmaeili's model. If directional motion energy predicted human performance, there should be no effect of connection between the three disks. However, the strong interaction observed in the connected condition suggests that perceived unity is crucial for non-retinotopic processing and that the two-stage model provides a better explanation of the results.

5.2. Dependence on retinotopic processing in pigeon vision

Contrary to the human results, we failed to find an interaction between ISI and the number of disks in pigeons in any experiment. The pigeons attended to the target location in all combinations of ISI and the number of disks. This does not mean that the pigeons viewed only the target, because task performance was affected by the appearance of the flanked inducers. The pigeons appear to depend on retinotopic coordinates, and never use non-retinotopic processing.

The dependence on retinotopic coordinates is highly relevant to the Gestalt laws of perceptual grouping in pigeons. Previous studies demonstrated that similarity and proximity of stimuli enhance the perceptual grouping in pigeons (Cook, 1992a, 1992b, 2001; Cook, Cavoto, & Cavoto, 1996). These results may be accounted by the dependence on retinotopic coordinates; proximate fragments in retinal images are grouped in pigeon vision. However, no previous study has found the law of common fate in pigeons

(Ushitani, Fujita, & Yamanaka, 2001). In human vision, stimuli moving in concert are grouped, even though they are located far apart or separated by other stimuli. This indicates that non-retinotopic processing precedes retinotopic one. The dependence on retinotopic coordinates in pigeons demonstrated in the present study predicts that law of common fate has little effect on perceptual grouping in pigeons.

The dependence on retinotopic coordinates in pigeons is also apparent in their kinematic behavior. When pigeons walk on the ground, their heads shift back and forth. Frost (1978) reported that these head movements consist of two phases, one in which the head is locked in space (but moves backward relative to the forward moving body), and the other in which the head is thrust rapidly forward to a new position. Frost suggested that pigeons lock their head in space so that the retinal images are stable. Our findings support this perspective. Even if retinal images shift, non-retinotopic processing does not compensate the image shifts because of the lack of non-retinotopic processing in pigeons. It is necessary for pigeons to lock their head in space because of heavy dependence on retinotopic coordinates.

5.3. What causes heavy dependence on retinotopic coordinates in pigeons?

In the pigeon brain retinotopic encoding is preserved in TeO (Mcgill, Powell, & Cowan, 1966), but not in the nRt (Marín et al., 2003). This tectofugal pathway is thought to correspond to the tectopulvinar-extrastriate pathways in primates (Karten & Shimizu, 1989), and the majority of retinal cells in the frontal visual field are projected into TeO (Remy & Güntürkün, 1991). The retinotopic structure of the pigeon visual system is quite similar to that in primates, in which simple point-to-point retinotopy is preserved only in the early visual areas (Tootell et al., 1998). However, we found no evidence of non-retinotopic processing by pigeons. The results suggest that visual information processing in pigeons heavily depends on retinotopic coordinates even in higher visual areas. Marín et al. (2012) showed that the feedback signal from the satellite nuclei to TeO selects which afferent activity propagates to the different subdivisions of the nRt. They showed that when a second moving stimulus appeared in the visual field, the feedback to the first stimulus location was abolished (though the first stimulus was still present), and new feedback started at the newly activated tectal location. Their results suggest that only selected tectal cells project onto the following nRt neurons; that is, stimulus selection occurs in early stages of visual processing in pigeons. In the present experiments, only the tectal location corresponding to the retinal target location could be selected and projected to the following regions. The early selection mechanism may causes the heavy dependence on retinotopic coordinates in pigeons.

This mechanism contrasts with the mechanism for motion processing in primates (Burr & Thompson, 2011 for review), in which local signals extracted in lower visual areas (e.g., striate cortex) are pooled and integrated in higher visual areas (e.g., extra-striate cortex). In the present experiments, local (target rotation) and global (group motion) motion signals were integrated in higher visual areas, and consequently the global signals interfered with the local signals in humans.

5.4. What is the origin of the non-retinotopic processing in humans?

Finally, we propose that the dependence on non-retinotopic coordinates is related to the properties of fixational eye movements of each species. The results of the present study suggest that non-retinotopic processing may not be widespread in animal kingdom. What is the origin of non-retinotopic processing in primates? When humans gaze at an object the eyes are never still; small involuntary eye movements always occur. These fixational eye movements continuously produce visual inputs and prevent neural adaptation. For keeping our perceptual world stable, however, non-retinotopic processing fills in the gaps between the retinal images of each fixational eye movements.

Fixational eye movement patterns are diverse across animal species (Martines-Conde & Macknik, 2008; for review). In primates the amplitude of fixational eye movements is larger and frequency is much higher than in other vertebrates (Martines-Conde & Macknik, 2008). In contrast, the amplitude and frequency of these events in pigeons are small and low (Nye, 1969). The large and frequent fixational eye movements may lead to non-retinotopic processing in primates, or an inverse relationship may be there. More data are required about non-retinotopic processing in various animal species from a range of taxonomic groups.

6. Conclusion

This is the first study to examine whether non-retinotopic processing exists in non-human animals, using variants of the Ternus–Pikler stimulus as a litmus test. The results showed that humans use both non-retinotopic and retinotopic motion processing in specific spatio-temporal interactions, whereas pigeons are restricted to retinotopic one. The contrasting results for the two species can be explained by structural difference in their respective visual systems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2014.08.007.

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